INHERITANCE OF SEX IN THE GRAPE[1]

W. D. VALLEAU

SECTION OF FRUIT BREEDING, UNIVERSITY OF MINNESOTA EXPERIMENT STATION, ST. PAUL, MINNESOTA

SINCE the discovery of Correns in 1907 that in *Bryonia* the staminate plants produce two kinds of gametes with respect to sex, and the pistillate and hermaphrodites only one, great advances have been made in the study of sex inheritance.

Shull (1910, '11, '14) has shown that in *Lychnis dioica* also the staminate plants are heterozygous for the sex genes, while the pistillate ones are homozygous, but that the hermaphrodites are heterozygous for the determiner for femaleness and for the hermaphrodite condition. These hermaphrodites were apparently developed from staminate plants as they bear only partially developed pistils in many flowers, and further, the factor for narrow leaves is linked with the determiner for the hermaphroditic condition, while in the normal males it is linked with that for maleness, as pointed out by Shull. Apparently the determiner for femaleness is carried suppressed and linked with the determiner for maleness in the staminate plants.

A simpler case of sex inheritance than either of the above is that of the sweet pea in which Bateson has shown that genotypically three kinds of plants may be produced; namely, the normal hermaphrodites, which produce only hermaphrodites when selfed, the pistillates bearing contabescent anthers, which when pollinated with pollen from the normal hermaphrodites produce the third type, which is phenotypically the same as the normal hermaphrodites. These when selfed produce hermaphrodites and pistillate plants in a 3:1 ratio, showing them to be heterozygous for

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the hermaphrodite and female determiners, and showing further that in the sweet pea only one dose of maleness is necessary for the production of functional stamens.

Similarly in many animals, it has been proved by Wilson, Morgan and others that the males are heterozygous for the sex determiner and the females homozygous, and that this condition is correlated with the presence of two chromosomes in the female which are distinct from the others and which they called the "X" bodies, while in the male only one may be present, or if there are two, the second is sometimes smaller and is spoken of as the "Y" body. Occasionally the X and Y bodies may be of equal size and the supposition that they are different is based upon inheritance studies.

The reverse of the above mentioned condition may exist, as in *Abraxis,* pigeons, cultivated fowl, etc., in which the males are apparently homozygous for the sex determiner and the females heterozygous.

Strasburger found that in *Bryonia* there were two chromosomes which were larger than the others and thought that these might carry the determiners for sex.

A great deal of evidence has recently been collected which points to the chromosomes as being the carriers of factors and as many factors have been shown to be linked with sex, it seems safe to conclude that certain chromosomes carry the determiner for sex. If this is the case, then in the hermaphroditic plants it must be assumed that the determiners for maleness and femaleness are linked or carried in the same chromosome; otherwise there would continually be produced not only hermaphrodites but staminate and pistillate plants as well.

The trend of development in many plant groups seems to be toward the production of a diecious condition by the suppression of the stamens in one set of individuals and of the pistils in another. As an instance of this may be cited the strawberry, in which staminate, pistillate and perfect flowers are produced. The grape and maple and many other plants show a like suppression in varying degrees.

Because of the number of flower types, and the fact that most of our cultivated grapes are only one or two generations from the wild, they would seem to furnish ideal material for the study of sex inheritance.

Two types of vines are found in the wild, those producing functionally pistillate flowers, but bearing reflexed non-functional stamens, and those producing functionally staminate flowers, but bearing suppressed pistils.

We have then apparently a transitional form, in the case of the grape, from a hermaphroditic condition such as is found in the apple, in which the male and female determiners are apparently linked, to the strictly diecious forms, as ashes, willows, etc., in which the determiner for maleness is completely suppressed in the sex chromosome bearing the determiner for femaleness, and the female determiner is completely suppressed in the chromosome bearing the factor for maleness.

On this hypothesis we would assume that in the functionally pistillate grape flowers the suppression of maleness has begun and evinces itself in the production of reflexed stamens bearing non-functional pollen, *i. e.*, lacking germ pores (Dorsey, 1913) and containing degenerate generative and vegetative nuclei embedded in apparently normal cytoplasm[2] (Gard, 1913). The period of degeneration of the nuclei is not at all definite. Rarely, the microspore nucleus does not divide. In some cases degeneration takes place directly following the microspore division, in others one nucleus only will degenerate at this time, and in still other cases the two nuclei will appear normal at the time of dehiscence (Dorsey, 1913). Beach (1899), Booth (1902) and Hedrick and Anthony (1915) have shown from pollination and germination tests that occasionally a few pollen grains borne in reflexed stamens are entirely functional. There is an apparent lack of suppression of maleness, occasionally, which allows the development of these normal grains.

Similarly it might be assumed that in the staminate

[2] Pollen of this type should not be confused with abortive pollen which is often produced in hybrids.

flowers suppression of the female determiner has taken place. Booth (1902) and Dorsey (1912) have shown that in practically all staminate grape flowers suppressed pistils are found. In some cases under cultivation and in rare instances in the wild state, the suppression of pistils is less marked and fairly well developed to perfectly developed pistils are formed. On individual plants occasionally all gradations from staminate to functionally hermaphroditic flowers are found.

A third type found under cultivation but which is extremely rare in the wild, is the functional hermaphrodite bearing all hermaphroditic flowers. A discussion regarding the probable origin of this type will be taken up later.

Although breeding work has been carried on for the past twenty-five or thirty years in this country with the grape, apparently little attention has been given to the inheritance of the various flower types, although a knowledge of sex inheritance would be of much value to the breeder. In 1914 Anthony published valuable data on sex inheritance in the grape, but gave no satisfactory interpretation of the results. In 1915 the data again appeared in more detail (Hedrick and Anthony, 1915), and, as no further attempt was made to interpret the results, the writer wishes to present the following as a probable explanation of sex inheritance in the grape, or at least as a working hypothesis for the interpretation of further results which may be obtained.

For the reason that in diecious plants there are apparently definite determiners for maleness as well as femaleness, while in animals it is supposed that males are produced when only one dose of the sex determiner is present, while females are produced if two doses are present, it seems well to use different symbols to designate the sex determiners of plants from those of animals. Therefore, those suggested by Shull (1914, p. 293) in which "the female is assumed to be a neutral homozygote," will be used in the following discussion, namely FF to represent a female and FM to represent a male.

The hermaphrodites would then be designated as $F\widehat{FM}$ or simply as FH. It will be seen from the following discussion that the only formulation which will meet the conditions is that which assumes the female to be a neutral homozygote.

In the above mentioned paper on the "Inheritance of Certain Characters of Grapes" (Hedrick and Anthony, 1915) the authors have concluded that the results obtained on inheritance of sex do not conform to the explanation of sex inheritance dependent on one sex being considered heterozygous and the other homozygous for sex determiners. It appears, however, that by using the hypothesis of partial suppression of sex determiners, the condition in the grape would be in accordance with the assumption of a homozygous condition for femaleness in the functional females, a heterozygous condition for maleness and femaleness in the functionally male plants, and a heterozygous condition for femaleness and hermaphroditeness in some of the hermaphrodites, while others would be homozygous for the hermaphrodite determiners. The authors based their conclusions upon the supposition that the hermaphrodites bearing upright and those bearing reflexed stamens were of a single type genetically, and produced only hermaphrodites and no females when crossed. This assumption seems erroneous.

Using the formulæ suggested above, let us apply them to the data given by the authors, which are as follows:

U × U[3] = 180 U + 47 R	R × R[3] = 16 U + 16 R
U selfed = 673 U + 152 R	R selfed = 94 U + 73 R
U selfed = 18 U + 0 R	
Total.....871 U + 199 R	Total.....110 U + 89 R
Ratio.....4.3 U : 1 R	Ratio.....1.2 U : 1 R

R × U = 207 U + 206 R
Ratio.... 1 U : 1 R
U × R?

Hermaphrodite female × pure male = 56 hermaphrodites + 51 males.

[3] "The pollen parent is always placed last." "U" refers to hermaphrodites bearing upright stamens which are usually functional. R refers to hermaphrodites bearing reflexed stamens which rarely produce functional pollen.

In the following discussion the term "female" will refer to the plants bearing morphologically perfect flowers but having reflexed stamens, the pollen of which is not functional. "Hermaphrodite" refers to those bearing perfect flowers, the stamens of which are upright and produce functional pollen. "Male" refers to those plants bearing staminate flowers.

The expectation from the cross "U × U" (hermaphrodite FH × hermaphrodite FH) would be 3 hermaphrodites: 1 female (FF); the hermaphrodites being of two types, viz., 2 FH : 1 HH. This ratio is very closely met in the figures 180 upright and 47 reflexed. "U selfed" should give the same proportions and these are closely approached in the figures 673 upright and 152 reflexed. This assumes the production of homozygous hermaphrodites (HH), which, when either selfed or crossed with other types, produce only hermaphrodites. Apparently the two hermaphrodites which produced 18 hermaphroditic seedlings only, when selfed, are of this genetic constitution. At the Minnesota Experiment Station four hundred seedlings of Beta, open to cross pollination, produced only hermaphroditic flowers; indicating that Beta must be homozygous for the hermaphrodite determiners.[4]

The crosses "R × R" and "R selfed" (female FF × female FF), producing both hermaphrodites and females, might be explained on the hypothesis already given, viz., that of partial suppression of the determiner for maleness in the chromosome bearing the determiner for femaleness.

It has already been pointed out that in the pistillate flowers bearing reflexed stamens, a series of pollen conditions, ranging from those in which the microspore nucleus does not divide, through those in which the generative nucleus aborts directly after the microspore division, to those in which a few normal functional pollen grains are

[4] In *Lychnis dioica* Shull has shown that homozygous hermaphrodites are never produced.

produced, has been found. This very evidently shows that variation in the amount of suppression of the determiner for maleness takes place in the determiner for sex of these normal grains. This normal pollen when used to pollinate pistillate flowers should give, in some cases, females bearing reflexed stamens and in others hermaphrodites, depending upon the extent to which suppression of maleness is lacking in the chromosome bearing the sex determiners of these normal pollen grains.

From the cross "R × U" (female FF × hermaphrodite HF) should be expected females (FF) and hermaphrodites (HF) in the proportion of 1:1. This ratio is met exactly in the cross "R × U" = 207 upright and 206 reflexed.

The following analysis, kindly furnished me by Mr. Anthony of the New York State Agricultural Experiment Station, of the cross "hermaphrodite female × pure male" which produced "56 hermaphrodites + 51 males," shows that both hermaphrodites and females were used as the female parent and that three kinds of males were used, namely, wild males, males one generation from the wild and "intermediates" (males bearing occasionally a few well developed pistils).

	Upright	Reflexed	Males
Hermaphrodite × wild male	7	6	9
Hermaphrodite × male (1 generation from wild)[5]	15	0	14
Female × male (1 generation from wild)[5]	10	3	7
Hermaphrodite × intermediate (origin unknown)	6	4	15
Female × intermediate (origin unknown)	0	1	3
	38	14	48[6]

The various combinations will be considered separately.

The cross hermaphrodite (FH) × wild male (FM) produced 7 hermaphrodites, 6 females and 9 males, somewhat approximating the expected ratio of 1 female (FF) : 1

[5] The result of hermaphrodite × wild male.

[6] These totals do not quite coincide with those given in the published data, as the parents of 7 of the vines were not certainly known and are therefore omitted.

hermaphrodite (FH) : 2 males (FM) and (MH). The male MH is an entirely new genotype but apparently can exist as shown by the next cross, in which a hermaphrodite was pollinated by a male derived from this cross. Fifteen hermaphrodites, no females and 14 males were produced, the expected ratio being (if a male of the type HM were used) 2 hermaphrodites (HF and HH) : 2 males (MH and MF). If a normal male of the constitution FM had been used on a hermaphrodite of the constitution HF we should expect to have produced 1 hermaphrodite (HF) : 1 female (FF) : 2 males (HM and FM). No females were produced. Again we might assume that the hermaphrodite used was of the constitution HH and that a normal FM male was used. In this case we should expect a 1 : 1 ratio of hermaphrodites and males as before, but in this case all of the males would be of the new type HM. It seems, therefore, that the production of this new male genotype (MH) must be admitted. Further evidence for the production of males of this type is produced in the cross female (FF) × male (one generation from wild) which produced 10 hermaphrodites, 3 females and 7 males. If the males used had been of the normal type FM only females and males could have been expected, as are found under wild conditions, and no hermaphrodites. If a male of the type HM were used, however, the expected ratio would be 1 hermaphrodite HF : 1 male FM. The presence of three females, although not expected, from the cross FF × HM can be readily explained, as it has already been pointed out that the males "one generation from the wild" are of the two genotypes FM and HM, but of one phenotype, and therefore could not be distinguished at the time of pollen collection.

The cross hermaphrodite × intermediate (origin unknown) which produced 6 hermaphrodites, 4 females and 15 males, throws some light on the genetic constitution of these intermediates and incidentally upon the suppression of femaleness. Observations on a number of "intermediates" produced at the Minnesota Fruit Breeding

Farm showed that certain clusters of a vine may be entirely staminate, while others of the same vine contain all gradations from staminate to functionally perfect flowers, many of which are capable of setting fruit. There is very evidently a suppression of femaleness in certain parts of these plants and not in others. This raises the question as to whether pollen from the pure staminate clusters can transmit only determiners for maleness and femaleness, or whether they are able to transmit the hermaphrodite condition. Mr. Anthony informs me that the pollen used in the above cross was "most certain to have come from such blossoms" (*i. e.*, from pure male clusters). If the two types of gametes produced by these flowers bear the determiners H and F, respectively, the cross hermaphrodite × intermediate should produce hermaphrodites and females in a 3:1 ratio and no males, while if these male flowers function as normal males and the gametes produced carry the determiners F and M respectively, a ratio of 1 hermaphrodite (HF) : 1 female (FF) : 2 males (HM and FM) would be expected. A close approximation to this ratio was actually produced.

The cross female (FF) × intermediate which produced 1 female and 3 males, gives further evidence that the staminate flowers of the intermediate vines do not produce gametes bearing the hermaphroditic determiner, but act as pure males. Otherwise the appearance of the three males can not be explained.[7] Although the number of vines produced from this cross is small, still the appearance of the three males is extremely significant.

It has already been pointed out that in the wild there are two types of vines, male and female, and that under cultivation a third type, the functional hermaphrodite, is common. We are now in a position to discuss the possible origin of these types. It is clear that both the staminate and functionally pistillate vines carry the determiners for femaleness and maleness, respectively,

[7] Anthony (1914) pointed out the fact that the pollen from these intermediates "seems to behave as the pollen of a pure male."

partially suppressed and therefore, there are two possibilities with regard to the origin of functional hermaphrodites. (1) Maleness may express itself fully in one of the chromosomes bearing the determiner for femaleness in a pistillate plant, and (2) femaleness may express itself fully in the chromosome bearing the male determiner in the staminate plant. I think it can be said definitely that functional hermaphrodites have been developed in both of these ways. The production of hermaphrodites from the cross female $\times$ female can hardly be explained on any other basis than entire lack of suppression of maleness in certain gametes bearing the female determiner, while the appearance of well-developed pistils in a few flowers of certain male vines must be the result of lack of suppression of femaleness in at least a portion of the somatic cells of these males.

As there is an apparent segregation in the somatic tissue of these vines, whole clusters and occasionally all clusters on a cane being staminate while others bear many intermediate and perfect flowers, it seems logical to assume that the perfect flowers can transmit the hermaphroditic condition to some of their seedlings through both the male and the female gametes, resulting in either homozygous or heterozygous hermaphrodites, all of whose flowers are perfect.

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